

**COLONY FOUNDATION AND PLEOMETROSIS IN *CAMPONOTUS*
(HYMENOPTERA: FORMICIDAE)**

ALEX MINTZER

Museum of Zool. and Division of Biol. Sci., Univ. of Michigan,
Ann Arbor, 48109

The period of reproductive activity and colony foundation is obviously crucial in the life cycle of ants. In most ant species, new colonies are established by independent females after a mating flight. The reproductives are subject to predation and the vagaries of weather during and after the mating flight, and the number of suitable sites for colony foundation available to individual dispersing females may be a limiting factor. The first worker brood is usually reared by the isolated female without any additional assistance. The females might increase the food reserves available for brood rearing by foraging outside the incipient nest, thereby increasing the individual size or number of workers in the first brood, but foraging behavior exposes the female to additional predators. Foraging by colony foundresses occurs only in a small number of ant taxa studied, notably in some Ponerinae and the Australian genus *Myrmecia* (Wheeler, 1933; Haskins, 1955), in some attines (Weber, 1972) and in acacia ants belonging to the genus *Pseudomyrmex* (Janzen, 1966). In most ant species, females do not forage and must rear a worker brood on a limited supply of food reserves. However, conspecific females may cooperate in jointly rearing a first brood; this is termed pleometrosis. Hölldobler and Wilson (1977) provide a recent review of pleometrosis in ants.

Pricer (1908) and Eidmann (1926) provide accounts of colony foundation in two species of *Camponotus* in the eastern United States and Europe. Their studies show that females of *Camponotus ligniperda* and *C. herculeanus* found colonies independently in a manner similar to most other ants. They do not seek food or capture prey outside their incipient nest chamber during colony foundation. *Camponotus* females apparently do not found colonies through temporary social parasitism involving other ant species, unlike some ant genera (Wilson, 1971).

This paper describes colony foundation in seven *Camponotus* species (representing four subgenera) in the western United States. The effect of an initial supplementary feeding on colony foundation success was investigated using two species of *Camponotus*. Five cases of successful colony foundation by pairs of cooperating females of *C. vicinus* are described.

Table 1. Collection data for ants used in study of colony foundation.

Species	No. females	Locality	Date
<i>Camponotus</i> (<i>Tanaemyrmex</i>) <i>vicinus</i> Mayr	1	Tehachapi Mtn. Park, Los Angeles Co., California	July 8, 1973
<i>C. vicinus</i>	4	Iowa Hill, Placer Co., California	May 1974
<i>C. vicinus</i>	7	Iowa Hill	May 1975
<i>C. vicinus</i>	14	Iowa Hill	May 2, 1976
<i>C. (Tanaemyrmex)</i> <i>festinatus</i> (Buckley)	1	Brawley, Imperial Co., California	July 24, 1974
<i>C. (Camponotus)</i> <i>modoc</i> Wheeler	1	Iowa Hill, Placer Co., California	May 1974
<i>C. (Camponotus)</i> <i>laevigatus</i> F. Smith	4	Iowa Hill	May 1974
<i>C. laevigatus</i>	5	Iowa Hill	May 1975
<i>C. laevigatus</i>	1	Flagstaff, Coconino Co., Arizona	May 10, 1974
<i>C. (Myrmentoma)</i> <i>clarithorax</i> Emery	1	Tustin, Orange Co., California	April 24, 1972
<i>C. (Myrmentoma)</i> <i>rasilis</i> Wheeler	2	Victoria, Victoria Co., Texas	May 8, 1974
<i>C. (Myrmentoma)</i> sp.	1	Pinery Valley, Chiricahua Mtns., Cochise Co., Arizona	Aug. 21, 1973
<i>C. (Myrmobrachys)</i> <i>planatus</i> Roger	4	Brownsville, Cameron Co., Texas	June 6–7, 1977

Materials and Methods

The dealate females were collected in California, Arizona, and Texas. Most were taken in the open, presumably at the conclusion of mating flights. Several females were found when the incipient nest chamber was broken open during routine collecting activity. Table 1 lists the collection data for ants used in this study.

Most of the females were housed in 35 mm plastic petri dishes lined with filter paper. Water was supplied periodically to all ants by wetting a cotton ball inserted through the plastic dish lids. The *C. planatus* females were kept in glass shell vials with cork stoppers. The dishes or vials containing founding females were kept together under a thin-wall cardboard box lid or in incubators to exclude light. Air temperatures ranged from 22 to 29°C during colony foundation.

Females collected in 1972, 1973, and 1974 were offered honeywater soon after capture, or as the first larvae neared maturity. In 1975, the effect of this initial feeding was tested using *C. vicinus* and *C. laevigatus*. Three females of each species were denied access to honeywater until the first workers eclosed. Two other females of each species received an initial *ad*

libitum feeding of honeywater shortly after capture. Honeywater was given to all incipient colonies within two days after eclosure of the first worker, and the cotton ball was removed from the petri dish lid to allow ants access to the exterior. Honeywater and insects were supplied on a regular basis once the worker offspring began foraging. Muscid and Calliphorid flies were accepted by most species, and *Drosophila* flies were taken by *C. clarithorax* and *C. (Myrmentoma)* sp. Mealworms (*Tenebrio molitor*) were accepted by *C. vicinus*, which rejected *Drosophila*. The ants and brood later emigrated or were transferred to wood or plaster nests with glass tops.

In 1975, two compatible *C. vicinus* females were placed in one 35 mm plastic petri dish. In 1976, four pairs of compatible *C. vicinus* females were placed in 35 and 60 mm petri dishes (two pairs in each dish size). All dishes and vials with founding females were examined several times each week to monitor the development of the first brood.

Results and Observations

I. Colony Foundation and Effects of Initial Feeding

Nearly all of the dealate females used in this study reared workers to maturity, and required 48 to 74 days to rear the first brood (see Table 2). During colony foundation most of the ants remained motionless for long periods of time (e.g., Fig. 1 is a multiple second time exposure). The females produced a clutch of eggs over a period of several days following installation in the culture containers. The size of this initial egg clutch varied greatly. In the *C. laevigatus* and *C. vicinus* series, the maximum size of the first egg clutch ranged from 9 to 16 for single queen replicates. In the *C. planatus* series, all females produced six eggs or less. The eggs of species in the subgenera *Camponotus*, *Myrmentoma*, and *Myrmobrachys* were elongate and cylindrical in shape. The eggs of the *Tanaemyrmex* species were broadly oval rather than elongate-cylindrical in shape. The eggs of some species showed striking changes in appearance during embryonic development, due to internal cell movement or migration and changes in the chorion, and eggs of different age could be easily distinguished.

First brood larval growth was usually uninterrupted and rapid. However, the last larvae to hatch in a brood were often 'held back' in the first instar, and usually did not complete development until the following year. The first instar larva is a common resting stage during periods of overwintering or food shortages in *Camponotus* (Mintzer, unpubl. observation; Hölldobler, 1961). In 1974, the *C. modoc* female and three of the *C. laevigatus* females tore loose pieces of filter paper to cover larvae spinning cocoons. Pupal mortality and abortive adult eclosure were uncommon.

The genus *Camponotus* is characterized by a polymorphic worker caste. The workers in the first broods always belonged to the minor subcaste, and

Table 2. Development of first brood during colony foundation.

Species	No. of replicates	Duration of immature stages (days)			Total
		First egg to first larva	First larva to cocoon spinning	First cocoon to first worker	
<i>C. modoc</i> 1974	1	21	13	21	55
<i>C. laevigatus</i> 1974	4	25	14	26	64 (58–69)
<i>C. laevigatus</i> 1975	5	20	12	20	55 (48–70)
<i>C. vicinus</i> 1973	1	22	NR	NR	74
<i>C. vicinus</i> 1974	4	24	14	28	66 (62–70)
<i>C. vicinus</i> 1975	6	21	13	23	58 (54–63)
<i>C. festinatus</i> 1974	1	NR	NR	NR	69
<i>C. clarithorax</i> 1972	1	33	NR	NR	67
<i>C. (Myrmentoma)</i> sp.	1	28 ± 2	14	26	68 ± 2
<i>C. planatus</i> 1977	4	28	12	17	57 (54–58)

showed little size variation. The number of workers produced in the first brood or in the first season varied widely between species, but was often quite similar within a replicate series (e.g., *C. vicinus* in 1974). As expected, the ants aided in tending the brood, but the queen did not abruptly relinquish

Table 3. Effects of an initial honeywater feeding on colony foundation.

Species/female		Treatment	Duration of immature stages (days)			Total	No. of workers + cocoons in first brood (August 15)
			First egg to first larva	First larva to cocoon spinning	First cocoon to first adult		
<i>C. vicinus</i>	BE	fed	20–21	12–14	23–25	58	10
	BF	fed	—	—	—	—	—
	BGX	unfed	25–26	13–14	23	63	10
	BHX	unfed	18–20	12–13	22	54–55	11
	'75	unfed	23	11–12	22–24	57–59	7
	BJX	unfed	17–18	14–15	22–23	55–56	7
Colonies founded by four females receiving initial honeywater feeding in 1974							7, 8, 9, 9
<i>C. laevigatus</i>	AE	fed	20–21	7–8	21	48	8
	AF	fed	18–19	11	18–20	47–50	10
	AGX	unfed	20–21	10–11	22	52	9
	AHX	unfed	19	17–18	19	56	7
	AIX	unfed	41 ^a	9	15–21	66–71	4
Colonies founded by four females receiving initial honeywater feeding in 1974							2, 4, 6, 6

^a Egg consumption by this female probably resulted in the longer egg stage duration observed.



Figs. 1–2. Fig. 1. Colony founding female of *Camponotus vicinus* with first larval brood. Fig. 2. Cooperating pair of *C. vicinus* females with first brood of larvae and cocoons.

brood care after the workers eclosed, and often participated in this activity throughout the first season. Workers in most colonies began foraging within 25 days following eclosure. The foraging workers were generally timid and retreated from any disturbance, although some ants tended to investigate the foraging arena during and after any manipulation, whether or not food was offered. Worker recruitment was occasionally observed in these small colonies during emigration or when honey was offered.

Table 4. First brood egg and worker production by single and paired females (1975, 1976).

		Maximum egg no.	No. of workers and cocoons
Single female	Range	9-16	1-11
Replicates	Mean	12.2	6.8
n = 9	Std. dev.	2.3	3.5
Paired female	Range	17-30	11-17
Replicates	Mean	20.4	13.8
n = 5	Std. dev.	5.5	2.6

Table 3 shows the results of the experiment testing the effect of initial feeding on colony foundation. One of these ants (female BF) was infertile and her eggs failed to hatch, even though she had received honeywater. All other ants reared brood to maturity. Egg eating was not observed among females which had received honeywater, although unaccounted loss of eggs was noted in one case (female AE). Egg eating by two unfed ants (AIX and BJX) was observed, and one egg was consumed in each case. One pupa disappeared and was presumably consumed by an unfed *C. laevigatus* female (AGX). The maximum size of the egg clutch was similar in the two groups, as was the brood development time and the number of workers in the first brood.

II. Cooperative Colony Foundation by Two Females

In 1975, a pair of *C. vicinus* females successfully reared a brood of 11 workers to maturity. The two ants maintained a single egg pile; the maximum size of this clutch was 21 eggs. In 1976, four pairs of *C. vicinius* successfully reared worker broods to maturity. Several pairing attempts were required to find compatible females for this experiment, as some combinations of the ants available led to fighting. One female lost three legs in such fights after initial pairing. However, paired females that were compatible in the initial stages during egg laying remained compatible for the entire period of colony foundation. Oral food exchange between females and allogrooming was observed, and 'dominance' or aversive behavior was very subtle or absent. Occasionally one female would climb partially on top of the second female, but biting was never observed (cf. *Polistes*; West-Eberhard, 1969) and the putative dominant-submissive roles were often reversed when the behavior was observed again. On May 21, an accident resulted in the loss of all eggs in the dishes, but all of the ants produced a second clutch. The paired females produced a single egg clutch, which was larger ($p < 0.01$, Behrens-Fisher t test) than the egg clutches of single foundress queens. The time period involved and the details of brood development were similar in single and paired-female series, but paired females produced

more workers than single females ($p < .005$, Behrens-Fisher t test). Females in 60 mm dishes did not rear more workers than did those in 35 mm dishes.

Three of the four pairs of females founding colonies in 1976 remained compatible through August 1977. One pair was separated after fighting between the females began in March 1977. The largest colony with two females had 42 worker offspring in early August 1977.

Discussion

The high proportion of females which successfully founded colonies is noteworthy. The culture dishes and vials satisfied a requirement for a small closed cavity during colony foundation, without contamination by pathogenic bacteria and fungi. The four subgenera of *Camponotus* surveyed in the study occupy different habitats in nature. Ants in the subgenus *Tanaemyrmex* nest in the soil in the western and southern United States. *Camponotus laevigatus* and *C. modoc* occur in forested mountain areas in western North America, and nest in large pieces of wood. The ants in the subgenus *Myrmentoma* are largely arboreal and are distributed throughout the United States and southern Canada. The subgenus *Myrmobrachys* is the dominant group of arboreal *Camponotus* in neotropical habitats, and occurs in the United States in southern Arizona, Texas, and Florida (Creighton, 1950).

Conditions in the laboratory probably minimized the brood development time. Water was supplied on a regular basis, and temperature extremes were avoided during colony foundation. Under these conditions, supplemental honey feeding had little or no effect on the first brood development time, and did not appear to increase the size of this brood. Brood cannot be satisfactorily reared on honeywater alone. However, the ants could use the sugars present in honey for some of their own metabolic needs, and thereby free more protein and lipid reserves for use in brood rearing. Such a facilitatory effect has been demonstrated in *Myrmica* (Brian, 1973). Under less satisfactory culture conditions, beneficial effects of the initial feeding might become apparent. Brood consumption was uncommon in the laboratory, but was more frequent among unfed females. In the field, lower average or fluctuating temperatures would probably prolong or interrupt brood development, especially in areas inhabited by *C. modoc* and *C. laevigatus*.

The successful foundation of colonies by pairs of cooperating *Camponotus* is significant. Only one other account (Stumper, 1962) of pleometrotic colony foundation by *Camponotus* females is available. Stumper's colony foundation experiments with *C. (Camponotus) vagus* Scopoli were plagued by a high level of brood cannibalism and none of his single-female replicates reared workers to maturity. However, his pair of compatible females was successful at rearing workers, and produced more brood than the single females. Paired or grouped females of *Lasius flavus* (Fabricius) rear more

brood to maturity in a shorter period of time, and have a higher survivorship rate than single females (Waloff, 1957). Pairs of compatible *C. vicinus* founding females also appear to rear larger broods than single females. It is not clear whether both females are contributing brood during colony foundation. Even if only one individual in a pair contributes eggs to the clutch, she can produce a correspondingly larger number of eggs, to be tended by two founding females. However, the origin of these eggs probably will not influence the ultimate reproductive success of cooperating females. The reproductive success of each female is determined by the number of reproductive females and males contributed by each when the colony reaches maturity, and by colony survivorship functions. The increased number of workers produced by paired females may have a major positive impact on survivorship of incipient polygynous colonies. Unrelated females may be expected to cooperate if their expected reproductive success is increased above the level for haplometrotic colony foundation. According to kin-selection theory, related females may be expected to cooperate in colony foundation under some conditions when unrelated females would not, as long as the inclusive fitnesses of the participating ants are increased (Hamilton, 1964). All of the *C. vicinus* females involved were collected in a single locality and it is possible that some are sisters. The behavior of the ants during pairing attempts suggests that they are discriminating on some basis, possibly residual odor cues from the parent colony.

Records of mature polygynous colonies of *Camponotus* in nature are uncommon. Hölldobler (1962) found some in *C. ligniperda*, where the females were hostile to each other and maintained separate territories in large colonies. In a series of experiments, he found that newly fertilized dealate females were usually incompatible, and those females which did cooperate failed to rear a first brood to maturity. Hölldobler concluded that polygynous colonies of this ant arise by adoption of females or mating within the colony. In August 1973, the author excavated a large colony of *C. (Tanaemyrmex) sansabeanus* (Buckley) with two dealate females near the Southwest Research Station of the American Museum of Natural History at Portal, Arizona. These ants have shown no aggressive behavior towards each other in the four years after collection of this colony. Both contribute eggs and egg eating by the queens has not been observed. It seems likely that polygynous colonies of this type could occasionally originate through cooperation between founding females.

Conclusion

Under laboratory conditions, *Camponotus* females required 48 to 74 days to rear a worker brood to maturity. The development of this brood was uninterrupted and supplemental honeywater feeding did not accelerate de-

velopment or increase the brood size. Queens of *Camponotus vicinus* may cooperate during colony foundation; females doing so increased the size of the first worker brood, although the development period was not appreciably shortened.

Acknowledgments

I thank Randy Oliver and Roy Snelling for collecting some of the ants used in this study, and George L. Hunt and Peter J. Bryant for providing space for the ant cultures at the University of California, Irvine. I also thank Roy Snelling, George Hunt, Michael M. Martin and Richard D. Alexander for constructive comments and criticism during preparation of this manuscript.

Literature Cited

- Brian, M. V. 1973. Feeding and Growth in the ant *Myrmica*. J. Anim. Ecol. 42: 37-53.
- Creighton, W. S. 1950. The Ants of North America. Bull. Mus. Comp. Zool., Harvard, v. 103.
- Eidmann, H. 1926. Die koloniegründung der einheimischen ameisen. Vergleich. Physio. 3: 776-826.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour II. J. Theoret. Bio. 7: 17.
- Haskins, C. P., and E. F. Haskins. 1955. The pattern of colony foundation in the archaic ant *Myrmecia regularis* H. Insectes Sociaux 2: 115-126.
- Hölldobler, B. 1961. Temperaturunabhängige rhythmische erscheinungen bei rossameisenkolonien (*Camponotus ligniperda* Latr. und *Camponotus herculeanus* L.). (Hym. Form.). Insectes Sociaux 8: 13-22.
- Hölldobler, B. 1962. Zur Frage der Oligogynie bei *Camponotus ligniperda* und *Camponotus herculeanus*. Z. Angew. Entomologie 49: 337.
- Hölldobler, B., and E. O. Wilson. 1977. The number of queens: an important trait in ant evolution. Naturwissenschaften 64: 8-15.
- Janzen, D. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20: 249-275.
- Markin, G. P., Collins, H. L., and J. H. Dillier. 1972. Colony founding by queens of the Red Imported Fire Ant, *Solenopsis invicta*. Ann. Entomol. Soc. Amer. 65: 1053-1057.
- Pricer, J. L. 1908. The life history of the Carpenter Ant. Bio. Bull., Woods Hole, Mass. 14: 177.
- Stumper, R. 1962. Sur un effet de groupe chez les femelles des *Camponotus vagus* (Scopoli). Insectes Sociaux 9: 329-333.
- Waloff, N. 1957. The effect of the number of queens of the ant *Lasius flavus* (Fab.) (Hym., Formicidae) on their survival and on the rate of development of the first brood. Insectes Sociaux 4: 391-408.
- Weber, N. A. 1972. Gardening Ants, the Attines. Mem. Amer. Philosoph. Soc., v. 92.
- West Eberhard, M. J. 1969. The social biology of polistine wasps. Misc. Pub. Mus. of Zool., Univ. of Michigan 140:1-101.
- Wheeler, W. M. 1933. Colony foundation among ants. Harvard Univ. Press.
- Wilson, E. O. 1971. The insect societies. Belknap/Harvard Univ. Press.